NERVOUS SYSTEM OF THE POLYCLAD FLATWORM *NOTOPLANA ATOMATA* (O.F. MÜLLER)

by

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Résumé

Le système nerveux de *Notoplana atomata* comprend plusieurs plexus : épidermique, pharyngien, subépidermique, sous-musculaire ventral et dorsal, parenchymatique. Le cerveau est réuni au plexus sous-musculaire. Les mécanismes de l'Évolution du système nerveux des Turbellariés sont discutés. Le système nerveux des Polyclades ne peut être considéré comme homologue de celui des autres Plathelminthes.

The evolution of nervous system must be regarded as one of the main trends in the animal evolution, the history of this process being one of the central problems of biology. In this concern, the turbellarian nervous system is of a special interest. With their phylogenetical position near the basement of the evolution of Bilateria, turbellarians display the main trends and roots of the evolutional centralization in the nervous apparatus.

The knowledge of characteristic features of the nervous system of polyclads is especially important for exposing phylogenetical relationships between different groups of platyhelminthes, as well as between turbellarians and other Bilateria; but the nervous system of those worms is studied very poorly (Lang, 1884; Hadenfeldt, 1929; Corréa, 1949; Turner, 1946; Koopowitz, 1973, 1974).

We investigated the nervous system of the acotylean polyclad *Notoplana atomata* on total preparations using the histochemical method of the revealing of the localization of acetylcholinesterase activity (Gerebtzoff, 1959); besides, we report here the results obtained with using the Champy-Maillet osmium tetroxide-zinc iodide technique (Clara, David, Maillet, 1968). All specimens of *Notoplana atomata* were collected on the White Sea near the Leningrad University biological station.

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The anatomy of the nervous system of N. *atomata*

The nervous system of *Notoplana atomata* consists of several plexus structures which display different degrees of histological differentiation. We propose to distinguish epidermal, subepidermal, ventral and dorsal submuscular, parenchymal and pharyngeal plexuses.

The nervous system of *N. atomata* includes a well-developed cerebral ganglion covered by a thin, but distinct capsule. The architectonics of the brain was previously studied by Hadenfeldt (1929), who described several types of ganglion cells as well as

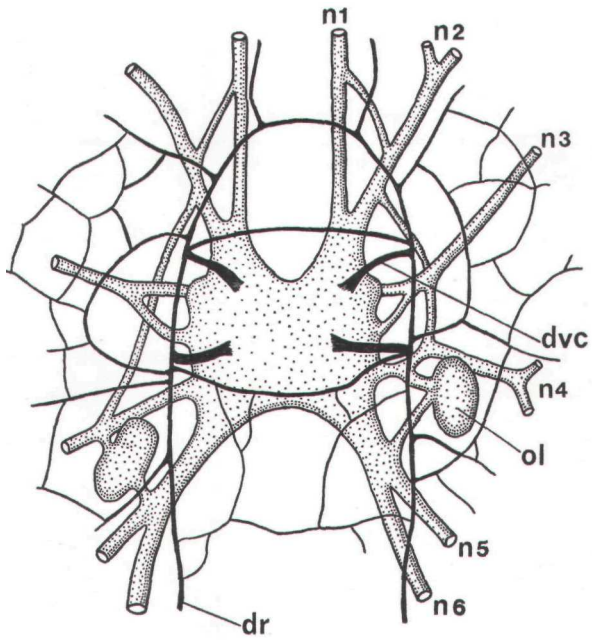

FIG. 1
Cerebrum and part of submuscular nervous systems of *Notoplana atomata*
dr: dorsal nervous ring (dorsal submuscular plexus); dvc: dorso-ventral commissure; n1-n6: nerves first-sixth pairs (n6: circumoral ring); ol: optical lobe.

certain structures of neuropile. In our material, similar histological relations were observed too. The brain is closely connected with the ventral submuscular plexus which, together with a less distinct dorsal one, composes the main part of the peripheral nervous system. The brain capsule is perforated by six pairs of nerves included into the network of ventral submuscular plexus, so that only their basal fragments can be called nerves in terms of morphology-

The basal part of two anterior pairs of nerves are brought together and connected by an oblique anastomose (Fig. 1). Each nerve of the third pair begins with two rootlets and makes anastom-

oses with a commissure connecting the first and the fourth pairs. Running alongside the brain, this coupled commissure emphasizes the radial symmetry in the central part of ventral submuscular plexus. On both sides, this commissure is connected with lateral brain lobes and with nerves of the fifth pair. Rootlets of the latter are united with those of the sixth pair. Besides, a pair of nerves, branching off the posterior lobes of the brain and leading to large optical ganglia, was observed.

The basis of ventral submuscular plexus is composed by the sixth pair of nerve cords connected with the brain. These are stretching backwards alongside the pharynx to unite when reaching the caudal body part. Four pairs of radial nerves are branching off these nerve cords. As a result, the circumoral nerve ring (including the brain) appears to be connected with ten pairs of radial nerves. All these nerves branch in a dichotomous way, thus composing a system of radially-settled meshes. The meshes of the

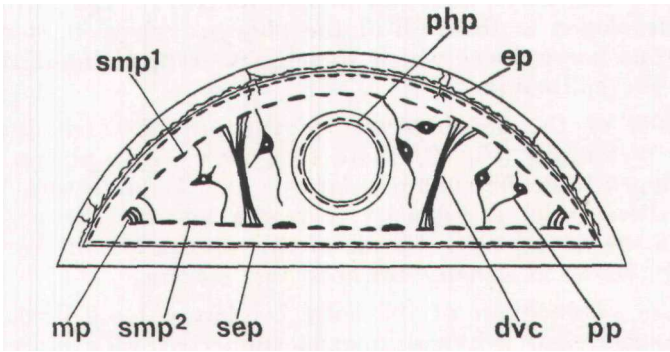

FIG. 2

Scheme of disposition of nervous plexuses of *N. atomata*

dvc: dorso-ventral commissure; ep: epidermal plexus; mp: marginal plexus; php: pharyngeal plexus; pp: parenchymal plexus; sep: subepidermal plexus; smp^1: dorsal submuscular plexus; smp^2: ventral submuscular plexus.

interior concentric line are displayed in a considerable order as to their size and localization, while those of the exterior lines seem to lose this regularity. The meshes are getting smaller towards the edge of the body. A dense nerve interlacement is formed in the zone of contact between ventral and dorsal plexuses. This marginal plexus is composed of plenty of short anastomosed dorsoventral commissures also (Fig. 2, mp).

The dorsal submuscular plexus is seen much less distinctly than the ventral one (Fig. 1; Plate 1, a, dr). The former is represented by an oblong nerve ring occupying the central zone of the dorsal surface. In their anterior parts both the nerve cords, that compose the dorsal ring, are connected by two commissures running over the brain. In points of their deviation, two pairs of delicate nerves are seen running towards the brain. Nerves of the anterior pair are connected with the central neuropile, while those of the posterior pair transverse the brain structures to unite with the nerve cords of the circumoral ring. At least six pairs of nerves

radiate from the dorsal ring. Their dichotomous branching picture is rather similar to what is seen on the ventral side but the strands of plexus on the dorsal side are more delicate and irregular.

The contacts between dorsal and ventral submuscular plexus systems are realized by three sorts of structures: 1. brain tracts, 2. marginal plexus and 3. dorsoventral commissures. At least four pairs of dorsoventral commissures connect dorsal and ventral nerve rings in points of deviation of radial nerves. The posterior couple of nerves connecting the dorsal ring and the brain may be considered as the fifth pair of these commissures. Other dorsoventral commissures are scattered irregularly all over the body.

The epidermal plexus was observed near the basement of the epithelium (Fig. 2; Plate 1, b, ep). It consists of long thin fibers running parallel to the basal membrane. However, in some places of the body, we failed to identify this plexus with the methods we applied. Peculiarities of this infra-epithelial nervous plexus have been studied lately by Chien and Koopowitz (1977). Epidermal plexus is most developed in the wall of the pharynx where it is composed of numerous nerve fibers which sometimes occupy almost the whole space of the epithelium.

Strands of the subepidermal plexus are observed just under the basal membrane (Fig. 2; Plate 1, c, sep). This plexus is much less developed than the submuscular one and its meshwork is denser on the ventral "side; the density increases towards the edge of the body. On the dorsal side, strands of this plexus are thicker without obvious increase in density towards the margin.

All the parenchyme of the body is pierced by delicate strands of the interior (parenchymal) plexus connected with large pseudo-unipolar neurones (Plate 1, d). The structure of the interior plexus is rather similar to that of other plexuses except its spatial (three-dimentional) disposition.

Thus, the peripheral nervous system of *N. atomata* consists of several relatively autonomous parts that display as it was stated above different levels of differentiation and might be of different origin. But there is no doubt that all the mentioned plexus systems are closely connected and compose an united morphodynamic complex.

One of the most amazing peculiarities of the nervous system of *N. atomata* (and apparently of all polyclads) is a combination of signs of high specialisation (as, for instance, their complex cerebral ganglion) with a primitive features (as presence of the epidermal plexus).

Notoplana atomata possesses well-developed sense organs. Without any detail description, we shall mention only their specific characteristics. The eyes are of three types: tentacle, brain extracapsular and brain intracapsular eyes. The first type eyes are situated on the surface of the special optical ganglia attached to the dorsal side of the body. Eyes of the second type are outside the brain capsule on the dorsal side, while those of the third type are dipped into the neuropile of the brain.

The anterior edge of the body carries a row of sensilles which

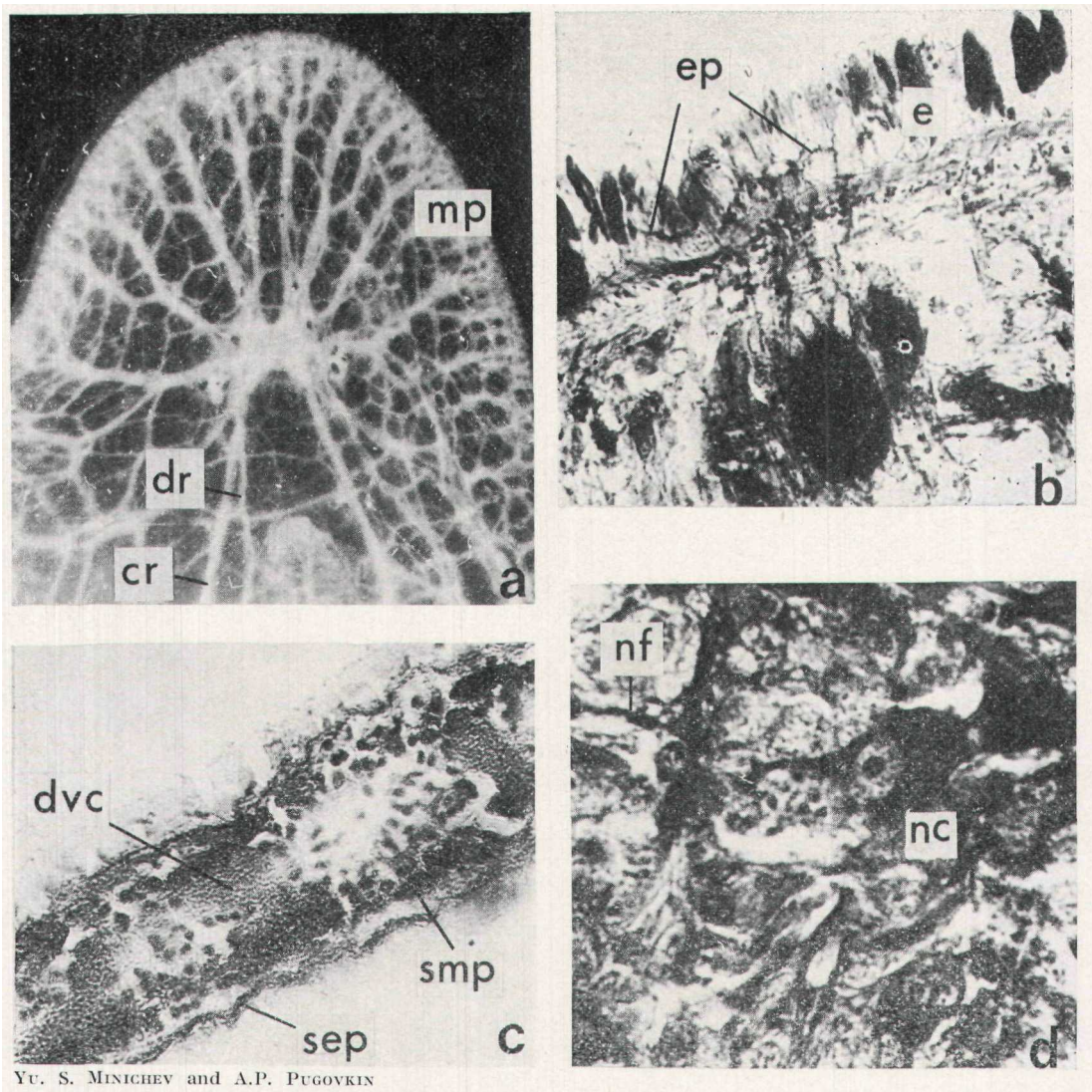

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PLATE 1

Nervous system **of** ***Notoplana atomata***

a. nervous system **of** anterior end (Gerebtzoff method), er: eireumoral nervous ring (sixth pair **of** ventral **submuscular cords);** dr: dorsal nervous ring (dorsal submuscular plexus); mp: marginal plexus.
oc. 7x, obj. 20x.

l). transversal section **of** worm (Champy-Maillet method); e: epidermis; ep: epidermal plexus.
oc. 7x, obj. 4()x.

c. sagittal section of worm **(Gerebtzoff** method), dvc: marginal dorso-ventral commissure; sep: subepidermal plexus; smp: submuscular plexus.
oc. 7x, obj. 40x.

d, parenchymal plexus (Champy-Maillet method), **ne:** nervous cell; nf: nervous fibre.
oc. 7x, obj. 90x.

are constructed apparently by the aggregated sensory neurons connected with the marginal plexus. Dorsal integument contains perceptive monocellular elements of somewhat primitive structure.

Discussion

The nervous system of *Notoplana atomata* displays some features seemingly common for polyclads but quite untypical for all other turbellarians. Among such features the presence of the epidermal plexus in combination with the immersed nerve cords is to be mentioned. Epidermal plexuses were observed previously only in some primitive acoelians and related groups (Ivanov and Mamkaev, 1973). Other turbellarians possess usually nervous system of the orthogonal pattern (Reisinger, 1925, 1972). In this case, polyclads differ both from primitive and specialized orders of Turbellaria. Nevertheless, the data on the structure of irregular epidermal plexus in Acoela remain rather scanty, so its further investigation in comparison with primitive nervous systems in other orders seems quite advisable.

The presence of the parenchymal plexus is another special feature of polyclads, as plexus structures of a similar kind occur only in some cestodes (Kotikova, 1976) being unknown in all other groups of platyhelminthes.

What are the reasons of differences in morphology of polyclads and other turbellarians? Beklemishev (1964) distinguished three types of nervous system development, that define correspond to the three levels of organisation among the Invertebrates. While Scolecida possess only ectodermic nervous system, entodermic and mesodermic elements are included respectively in nervous apparatuses of Trochozoa and Deuterostomia. It seems probable that these three large groups of animal kingdom are of different origin and that their ancestral forms possessed different levels of epithelisation in their germ layers. Ancestors of turbellarians might have an amorphous irregular phagocytoblast (primary entomesoderm) while those of Trochozoa and Deuterostomia could possess a progressive epithelisation of the interior (gastral) and peripheral (coelomic) phagocytoblast.

Evidence about the presence of mesodermic elements in the nervous system of *Notoplana atomata* may help to specify the phylogenetic relationships between primary germ layers and nervous system. In our opinion, differences between two groups of turbellarians appeared as a consequence of differences in structure and function of phagocytoblast in their ancestral forms.

In primary acoelians which seem to be regarded as ancestors of all turbellarians except polyclads the whole phagocytoblast participated in digestion so that mechanisms responsible for this function were connected with a specific dynamic state of parenchyma (Mamkaev and Seravin, 1963; Boguta and Mamkaev, 1972). In the ancestral polyclads, digestion took place mostly in the central part of the phagocytoblast. Morphological stability of the peripheral

phagocytoblast conditioned the apparition of the nervous elements of its own. The majority of contemporary turbellarians have not got any entodermic or mesodermic nervous structures so their internal organs are innervated by the ectodermic nervous system. In some triclads however, nerve fibers adjoining the gastroderm have been observed (Baguná, 1974), but their origin and phylogenetic significance are still vague. This gastrodermic nerve layer may be nothing more but deeply-sunken derivation of the primary ectodermic plexus.

Another characteristic feature of polyclads lies in structural differences between their nervous system and typical orthogon. Nervous system of the orthogon pattern is constructed by a set of longitudinal nerve cords connected by commissures (Reisinger, 1925, 1972; Hanström, 1928; Beklemishev, 1964). This nerve grating possesses high level of regularity and radial symmetry relating to the anteroposterior axis. Orthogon seems to be a result of the simultaneous concentration of nervous elements (associative and motor neurons together with their neuntes) in the course of spatial differentiation of the primary nerve plexus. During the first stage, longitudinal nerve cords have been differentiated while differentiation of regular commissures took place much later. These processes were followed by the immersion of the whole nervous system after which only the primary perceptive structures remained within the epithelium.

As to submuscular plexus in *N. atomata,* it seems to be of quite a different construction possessing the radial symmetry in relation to the dorsoventral axis, without any longitudinal stems except those composing circumoral and dorsal rings. In the nervous system of polyclads contact between dorsal and ventral part is performed by a special marginal plexus and dorsoventral commissures whereas in other turbellarians it is realized by a system of transversal commissures.

The structure of the cerebral ganglion in polyclads has some peculiarities to be mentioned. The presence of coupled optical ganglia outside the brain capsule as well as intracapsular eyes inside it indicates its phylogenetic relationship to the dorsal side though the brain itself is a structural part of the ventral nerve ring and topographically is attached to the ventral part of the nervous system. This is emphasized by the position of the anterior uncoupled branch of the intestine running straight above the medial scissure of the brain. The immediate connection between the dorsal part of the nervous system and the brain is carried out only by two pairs of rather fine commissures. A special embryological investigation might be necessary for the explanation of such an unusual phenomenon.

Independent phylogenetic formation of nervous systems on the basis of primary irregular plexus was shown by Reisinger (1972) in Protostomia and Deuterostomia. We adduced some arguments for phylogenetic independence in the formation of the nervous system in Annelida where nerve lattice of a special kind, designated as orthogonoid, has been developed (Minichev and Bubko, 1973). By the analogy with the organization of acoelians, primary turbell-

arians might possess an irregular epidermal nervous plexus. Its centralisation and immersion under the epithelium took place without doubt repeatedly in different evolutionary lines sometimes even within the limits of an order usually yielding a system similar to a typical orthogon pattern. We believe that the reported peculiarities of *N. atomata* prove that the direction of the evolution of the polyclad nervous system was quite different. It means that nervous system of polyclads and of other flatworms are not homologous to each other in spite of the fact that their evolutionary development is based on similar primary (diffuse) plexuses.

Summary

The nervous system of *Notoplana atomata* consists of several plexuses: epidermal, pharyngeal, subepidermal, ventral and dorsal submuscular and parenchymal. The brain is connected with the ventral submuscular plexus. Possible ways of the evolution of the turbellarian nervous system are discussed. The nervous system of polyclads and of other flatworms are not homologous.

Резюме

Нервная система *Notoplana atomata* состоит из нескольких плексусов: эпидермального (и глоточного), субэпидермального, вентрального и дорсального субмускулярных и паренхимального. Головной мозг связан с вентральным субмускулярным плексусом и топографически принадлежит брюшной стороне тела. Обсуждаются возможные направления эволюции нервной системы у турбеллярий. Выскаана гипотеза о том, что нервный субмускулярный плексус не гомологичен ортогону других турбеллярий.

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